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Redescription of Two Nematode Species Parasitic in the Japanese Clawed Salamander, *Onychodactylus japonicus* (Amphibia: Caudata: Hynobiidae), with Proposal of a New Genus *Shunyanema* (Nematoda: Oxyuroidea: Pharyngodonidae)

Hideo Hasegawa¹ and Akihiko Uchida²

¹ Department of Infectious Diseases, Faculty of Medicine, Oita University, Hasama, Yufu, Oita, 879-5593 Japan

E-mail: hasegawa@med.oita-u.ac.jp

² Department of Environmental Health, College of Environmental Health, Azabu University, Fuchinobe, Kanagawa, 229-8501 Japan

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Two species of parasitic nematodes, both associated with the Japanese clawed salamander *Onychodactylus japonicus* (Houttuyn, 1782) (Caudata: Hynobiidae), are treated in this paper. The first, *Angiostoma onychodactyla* Bursey and Goldberg, 2000 (Rhabditoidea: Angiostomatidae), is redefined as having an elliptical oral aperture without lips; double lateral alae; and male caudal papillae comprising nine pairs of pedunculate papillae, a single sessile papilla anterior to the anus, and two minute projections on the posterior anal lip. A new genus, *Shunyanema*, is established for *Parapharyngodon japonicus* Bursey and Goldberg, 1999 (Oxyuroidea: Pharyngodonidae). The new genus is characterized by the didelphic amphidelphic genital system, the vulva situated in the middle region of the body, and the anteriorly directed vagina in females; the absence of a V-shaped sclerotized structure supporting the genital cone in males; and the lack of an operculum and filaments in the eggs. *Shunyanema japonicum* comb. nov. is also redescribed and illustrated in detail.

Key Words: Nematoda, Angiostomatidae, Pharyngodonidae, *Shunyanema*, new genus, new combination, redescription, parasite, salamander, Japan.

Introduction

The Japanese clawed salamander, *Onychodactylus japonicus* (Houttuyn, 1782) (Caudata: Hynobiidae) is an endemic amphibian of Japan (Sengoku *et al.* 1996). Helminthological studies of this salamander have been made since the 1930s (Wilkie 1930; Pearse 1932). In 1986 we reported two parasitic nematodes, *Thelandros* sp. and *Angiostoma* sp., from specimens of this salamander collected in Hinoemata, Fukushima Prefecture (Hasegawa and Uchida 1986), although formal proposal of new taxa was withheld because of the poor condition of the available specimens. Later, Bursey and Goldberg (1999, 2000) described *Parapharyngodon japonicus* Bursey and Goldberg, 1999 and *Angiostoma onychodactyla* Bursey and Goldberg, 2000, both from *O. japonicus* collected in the same locality, Hinoemata.

Because of the presence of nematodes of the same or closely-related genera in

the same host species from the same locality, we suspected that the two nematode species reported by Hasegawa and Uchida (1986), *Thelandros* sp. and *Angiostoma* sp., were conspecific with the two species described by Bursey and Goldberg (1999, 2000), *P. japonicus* and *A. onychodactyla*, respectively, although there are considerable differences between the respective descriptions. Recently we had an opportunity to examine parasitic nematode material collected from *O. japonicus*, in which two species are represented. Detailed examination of the newly obtained material and a comparison with the paratypes of the two species described by Bursey and Goldberg (1999, 2000) have confirmed the above supposition; furthermore, it has been found that the original descriptions of the two species contained mistakes or inaccuracies in some important characters. Herein we redescribe the two species based on our own specimens in order to understand their morphology more precisely. In addition, a new genus *Shunyanema* is proposed for *P. japonicus*, because this species is distinct from any known species of *Parapharyngodon*. The relationships of the new genus to other pharyngodonid genera are discussed.

Materials and Methods

The newly obtained specimens were collected by Dr Takeshi Shimazu, Nagano Prefectural College, Nagano, Japan. They were fixed in hot 10% formalin solution, and preserved in the same solution. The specimens studied by us previously (Hasegawa and Uchida 1986) were also re-examined. All specimens were cleared in glycerol-alcohol solution by evaporation of ethanol, and mounted on glass slides in 50% glycerol aqueous solution. They were observed under a Nikon light microscope with Nomarski interference contrast. Figures were made using a Nikon drawing tube. Measurements, with mean and range in parentheses, are given in micrometers unless otherwise stated. Voucher specimens have been deposited in the Meguro Parasitological Museum, Tokyo, Japan (MPM).

The following specimens borrowed from the United States National Parasite Collection (USNPC) were also observed for comparative purposes: paratypes (7 males and 8 females) of *Angiostoma onychodactyla* from *Onychodactylus japonicus* of Hinoemata, Fukushima, Japan, USNPC 88647; paratypes (2 males and 8 females) of *Parapharyngodon japonicus* from *Onychodactylus japonicus* of Hinoemata, Fukushima, Japan, USNPC 88240.

Taxonomy

Superfamily Rhabditoidea

Family Angiostomatidae

Angiostoma onychodactyla Bursey and Goldberg, 2000 (Figs 1–10)

Angiostoma sp.: Hasegawa and Uchida 1986: 141.

Angiostoma onychodactyla Bursey and Goldberg, 2000: 60, figs 1–9.

Material examined. Ten males and 10 females, host *Onychodactylus japonicus*

from Utsukushigahara, Matsumoto, Nagano Prefecture, Honshu Island, Japan, 3 June 2003, collected by Takeshi Shimazu, MPM Coll. No. 18821; 9 males and 30 females, host *O. japonicus* from Hinoemata, Fukushima, Japan, 25 May 1976, collected by Akihiko Uchida, MPM Coll. No. 18824.

Redescription. Body soft, filiform. Sexual dimorphism not prominent. Cuticle with faint transverse striations. Double lateral alae present in both sexes, commencing anterior to nerve ring (Figs 1, 3, 7–9). Oral aperture elliptical, lacking lips (Fig. 2). Head papillae comprising of 6 inner and 6 outer circle papillae and 4 cephalic papillae (Fig. 2). Amphidial pores close to lateral outer circle papillae (Fig. 2). Buccal cavity thick-walled (Fig. 1). Esophagus with posterior pseudobulb without valve (Fig. 1); nerve ring immediately anterior to pseudobulb. Excretory pore near level of esophago-intestinal junction; deirids round, slightly posterior to excretory pore (Figs 1, 4).

Male (10 worms from MPM 18821). Subventral lateral alae terminating anterior to anus; subdorsal lateral alae terminating at anal level (Fig. 6). Body length 4.31 (3.91–4.82) mm, width 98 (88–107) at midbody. Buccal cavity 13 (12–14) long by 18 (16–20) wide including wall. Esophagus 308 (288–338) long, 24 (22–26) wide in corpus, 18 (16–18) wide in isthmus, and 37 (34–45) wide in pseudobulb. Nerve ring 241 (221–262), excretory pore 328 (294–381), and deirids 345 (310–422) from cephalic end. Caudal alae supported by 9 pairs of pedunculate papillae: first pair preanal, second to sixth pairs grouped just posterior to anus; seventh to ninth pairs, nearly equal-spaced, located in posterior half of tail; fifth and eighth pairs directed laterally slightly (Figs 5, 6). Unpaired sessile median papilla on anterior anal lip; pair of small projections on posterior anal lip (Figs 5, 6). Spicule well sclerotized, curved ventrally, 167 (156–180) long (Figs 5, 6). Gubernaculum oval, indented distally, 47 (42–51) long (Fig. 5). Tail 88 (83–99) long.

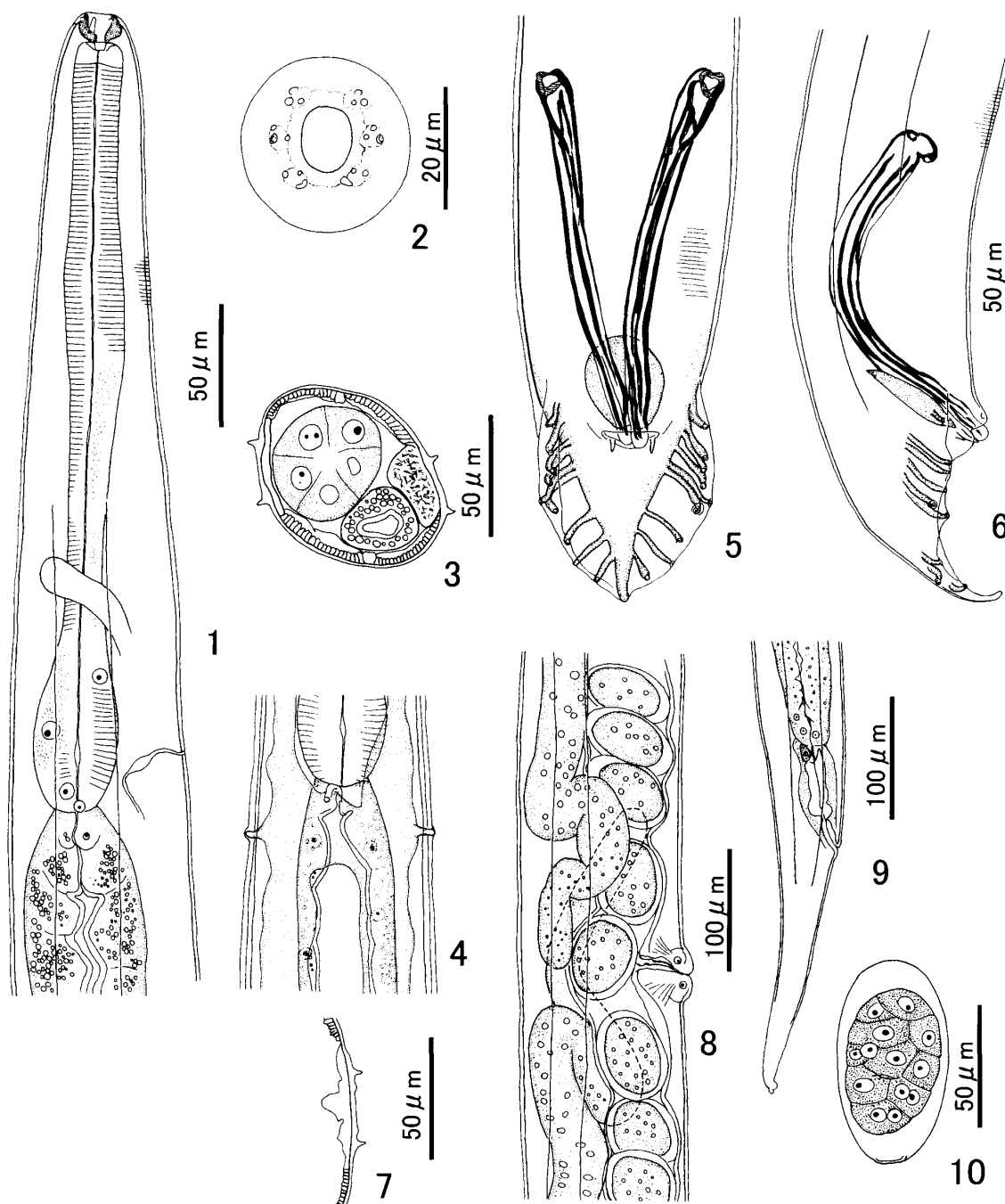
Female (10 worms from MPM 18821). Both subventral and subdorsal lateral alae terminating just posterior to anus (Fig. 9). Body length 5.41 (5.06–5.95) mm, width 117 (106–126) in midbody. Buccal cavity 13 (11–14) long by 19 (18–21) wide including wall. Esophagus 331 (304–371) long, 25 (24–26) wide in corpus, 19 (16–21) wide in isthmus, and 40 (37–45) wide in pseudobulb. Nerve ring 254 (237–266), excretory pore 339 (318–358), and deirids 356 (322–378) from cephalic end. Vulva in midbody, 2.70 (2.56–2.94) mm from cephalic end. Amphidelphic; ovijector weakly developed; anterior and posterior ovaries terminating near vulva (Fig. 8). Tail conical, 200 (176–214) long, often with 2 terminal tubercles (Fig. 9). Eggs in uteri ellipsoidal, thin-shelled, 64–83 by 34–49, containing morula-stage embryos at deposition. Eggs excised from uteri ellipsoidal, 78–86 by 44–46 (Fig. 10), shell with short, thickened bar on one pole.

Host. Japanese clawed salamander, *Onychodactylus japonicus*.

Site of infection. Small intestine and stomach.

Distribution. Hinoemata, Fukushima, Honshu Island, Japan; Utsukushigahara, Matsumoto, Nagano Prefecture, Honshu Island, Japan.

Remarks. The presence of a species of *Angiostoma* in *Onychodactylus japonicus* from Hinoemata, Fukushima Prefecture, was first reported by Hasegawa and Uchida (1986). Later, Bursey and Goldberg (2000) described a new species, *A. onychodactyla*, from *O. japonicus* collected in the same locality. Reexamination of the specimens referred to *Angiostoma* sp. by Hasegawa and Uchida (1986) has shown that they represent *A. onychodactyla*; however, there are discrepancies in some im-



Figs 1–10. *Angiostoma onychodactyla* Bursey and Goldberg, 2000, non-type, MPM Coll. No. 18821, from the Japanese clawed salamander, *Onychodactylus japonicus*. 1, Anterior portion of male, right lateral view; 2, cephalic end of male, apical view; 3, cross section in midbody of male; 4, esophago-intestinal junction area of male, ventral view; 5, posterior end of male, ventral view; 6, posterior end of male, right lateral view; 7, lateral alae in cross section of female midbody; 8, vulval region, right lateral view; 9, posterior end of female, right lateral view; 10, egg excised from uterus.

portant characters between the original description of *A. onychodactyla* and our own specimens. Bursey and Goldberg (2000) defined *A. onychodactyla* as having three oral lips and lacking lateral alae. The lips figured in the original description are in the form of slender projections, thus being quite unusual as lips, because in other species of *Angiostoma* the oral aperture is round or subtriangular and lacks lips (cf. Morand 1986; Morand and Spiridonov 1989; Morand and Barker 1995). Our observation of the paratypes of *A. onychodactyla* revealed the same morphology of oral structure and double lateral alae as redescribed above. Bursey and Goldberg (2000) did not mention the thick wall of the buccal cavity, paired small projections on the posterior anal lip, preanal pedunculate papillae, and deirids, which are often observed in *Angiostoma* spp. (cf. Morand 1986; Morand and Spiridonov 1989; Morand and Barker 1995). Presence of these structures was readily confirmed by our observation of the paratypes.

Superfamily Oxyuroidea
Family Pharyngodonidae
Shunyanema gen. nov.

Diagnosis. Sexual dimorphism prominent. Cephalic end with 3 lips, 6 labial papillae, and 4 cephalic papillae. Amphids not elevated on surface. Buccal cavity rudimentary. Esophagus with posterior bulb with sclerotized valve. Polymorphism present in males. Genital papillae of male consisting of anterior group around anus and posterior pair on tail. Male tail not reduced to slim appendage, and directed almost parallel to longitudinal axis of body. Posterior anal lip of male lacking V-shaped sclerotized structure; 3 pairs of small papillae around anus, 1 of which situated laterally; spicule simple. In females, vulva in middle region of body; vagina directed anteriorly. Didelphic, amphidelphic. Eggs without operculum and filaments. Parasitic in amphibians.

Type species. *Parapharyngodon japonicus* Bursey and Goldberg, 1999, present designation, by monotypy.

Composition. Only the type species.

Etymology. The generic name is dedicated to the late Mr Shunya Kamegai, former director of the Meguro Parasitological Museum, Tokyo, Japan. Gender: neuter.

Remarks. Our study has revealed that *Parapharyngodon japonicus* differs from all known congeneric species, all of which have a prodelphic genital system in females, thus warranting the establishment of a new genus for the former species. *Shunyanema* appears rather close to *Ataronema* Hasegawa, 2005, *Cithariniella* Khalil, 1964, *Mehdiella* Seurat, 1918, *Parathelandros* Baylis, 1930, *Skrjabinodon* Inglis, 1968, *Spauligodon* Skrjabin *et al.*, 1960, and *Synodontisia* Petter *et al.*, 1972 in having an amphidelphic genital system in females. However, the new genus is easily distinguished from *Ataronema*, *Parathelandros*, *Skrjabinodon*, and *Spauligodon* by the vulva opening in the midbody (cf. Skrjabin *et al.* 1960; Inglis 1968; Bursey *et al.* 1997; Hasegawa 2005); from *Cithariniella* and *Synodontisia* in having amphids not jutting prominently and non-filamented eggs (Petter *et al.* 1972; Anderson and Lim 1996); and from *Mehdiella* by lacking a well-developed, V-shaped, sclerotized structure supporting the posterior anal lip in males (Petter

and Quentin 1976). Bursey and Goldberg (1999) stated that the eggs of their *Parapharyngodon japonicus* were operculate, but the supposed operculum appears to be nothing more than a slightly thinner portion of the shell near the pole, a condition that is clearly different from the operculum with a distinct rim found in the eggs of other species of *Parapharyngodon* (Adamson 1981).

Shunyanema japonicum (Bursey and Goldberg, 1999), comb. nov.
(Figs 11–22)

Thelandros sp.: Hasegawa and Uchida 1986: 141.

Parapharyngodon japonicus Bursey and Goldberg, 1999: 181, figs 1–6.

Material examined. Five males and 10 females, host *Onychodactylus japonicus* from Hinoemata, Fukushima, Japan, 25 May 1976, collected by Akihiko Uchida, MPM Coll. No. 18822, and 17 June 2003, collected by Takeshi Shimazu, MPM Coll. No. 18823.

Redescription. With the generic characters defined above. Body minute. Cuticle with coarse transverse striations. Cephalic papillae with irregular contour (Fig. 18). Nerve ring at posterior portion of corpus (Figs 10–13, 17, 20); excretory pore posterior to esophago-intestinal junction.

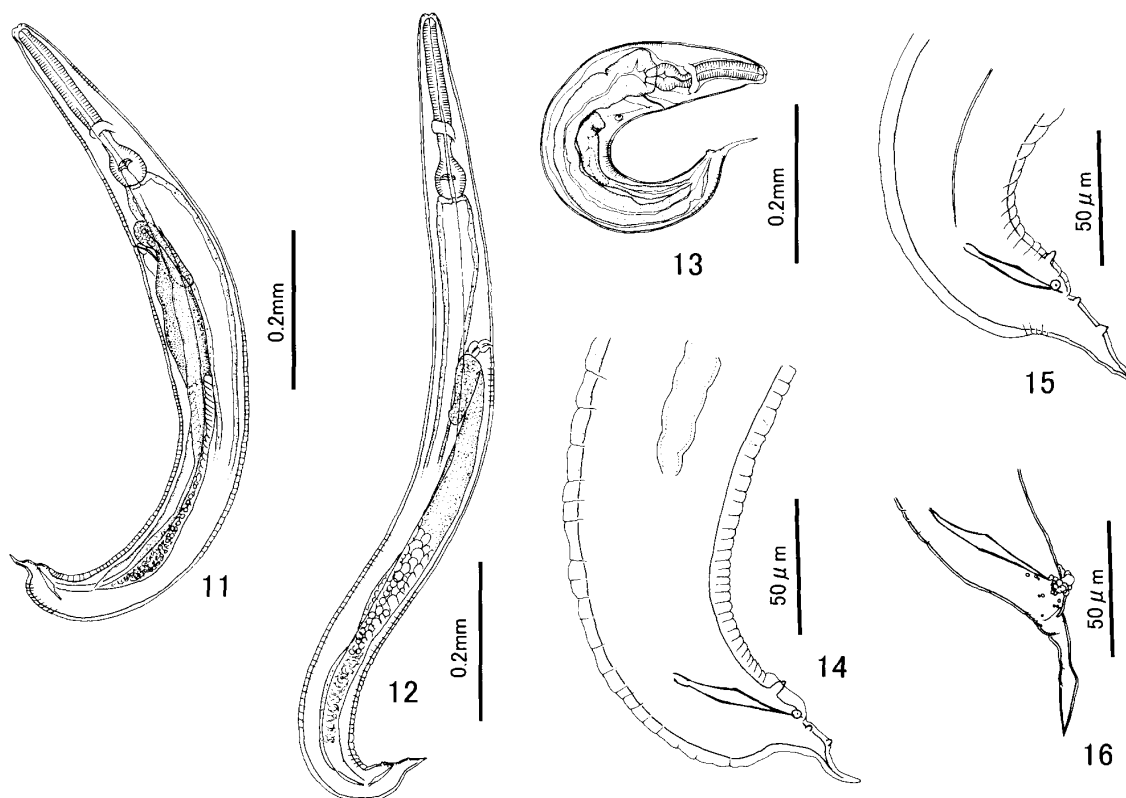
Male. Three morphs are recognized.

Morph I (3 worms). Lateral alae prominent, 19 wide in midbody, commencing at level of nerve ring, terminating anterior to anus (Figs 11, 14). Body length 0.98 (0.94–1.06) mm, width 101 (95–106) at midbody. Esophagus 214 (195–230) long, 22 (19–26) wide in corpus, 15 (15–16) wide in isthmus, and 41 (39–42) wide in bulb. Nerve ring 163 (138–179), excretory pore 269 (266–272) (n=2) from cephalic end. Caudal alae absent; 4 pairs of sessile caudal papillae, i.e., 1 pair preanal, 1 pair adanal, and 2 pairs postanal (Fig. 14). Spicule widened at middle, sharply pointed distally, 49 (45–54) long (Fig. 14). Body narrowed posterior to anus to form long, conical tail of 36 (32–40) long (Fig. 14).

Morph II (1 worm). Lateral alae narrow, 6 wide in midbody, commencing at level of nerve ring, terminating anterior to anus (Fig. 12). Body length 1.11 mm, width 80 at midbody. Esophagus 224 long, 21 wide in corpus, 14 wide in isthmus, and 40 wide in bulb. Nerve ring 165, excretory pore 286 from cephalic end. Caudal alae absent; 4 pairs of sessile caudal papillae, i.e., 1 pair preanal, 1 pair adanal, and 2 pairs postanal (Fig. 15). Spicule widened at middle, sharply pointed distally, 40 long (Fig. 15). Tail tapering gradually, 42 long (Fig. 15).

Morph III (1 worm). Lateral alae absent. Body length 0.59 mm, width 93 at midbody (Fig. 13). Esophagus 144 long, 20 wide in corpus, 14 wide in isthmus, and 35 wide in bulb. Nerve ring 85, excretory pore 138 from cephalic end. Caudal alae absent; perianal region with many round formations of irregular size. Spicule widened at middle, sharply pointed distally, 50 long (Fig. 16). Tail tapering gradually, 58 long (Fig. 16).

Female (10 worms). Lateral alae absent. Body length 2.92 (2.13–4.17) mm, width 323 (230–462) in midbody (Figs 17, 20). Esophagus 416 (358–449) long, 42 (35–51) wide in corpus, 30 (26–37) wide in isthmus, and 90 (80–107) wide in bulb. Nerve ring 234 (208–253), excretory pore 703 (509–891) from cephalic end. Vulva slightly posterior



Figs 11–16. *Shunyanema japonicum* (Bursey and Goldberg, 1999), comb. nov., non-type male, from the Japanese clawed salamander, *Onychodactylus japonicus*. 11, 14, Morph I, MPM Coll. No. 18823; 12, 15, morph II, MPM Coll. No. 18823; 13, 16, morph III, MPM Coll. No. 18822. 11–13, Entire worm, left lateral (11) or right lateral (12, 13) views; 14–16, posterior end, right lateral view.

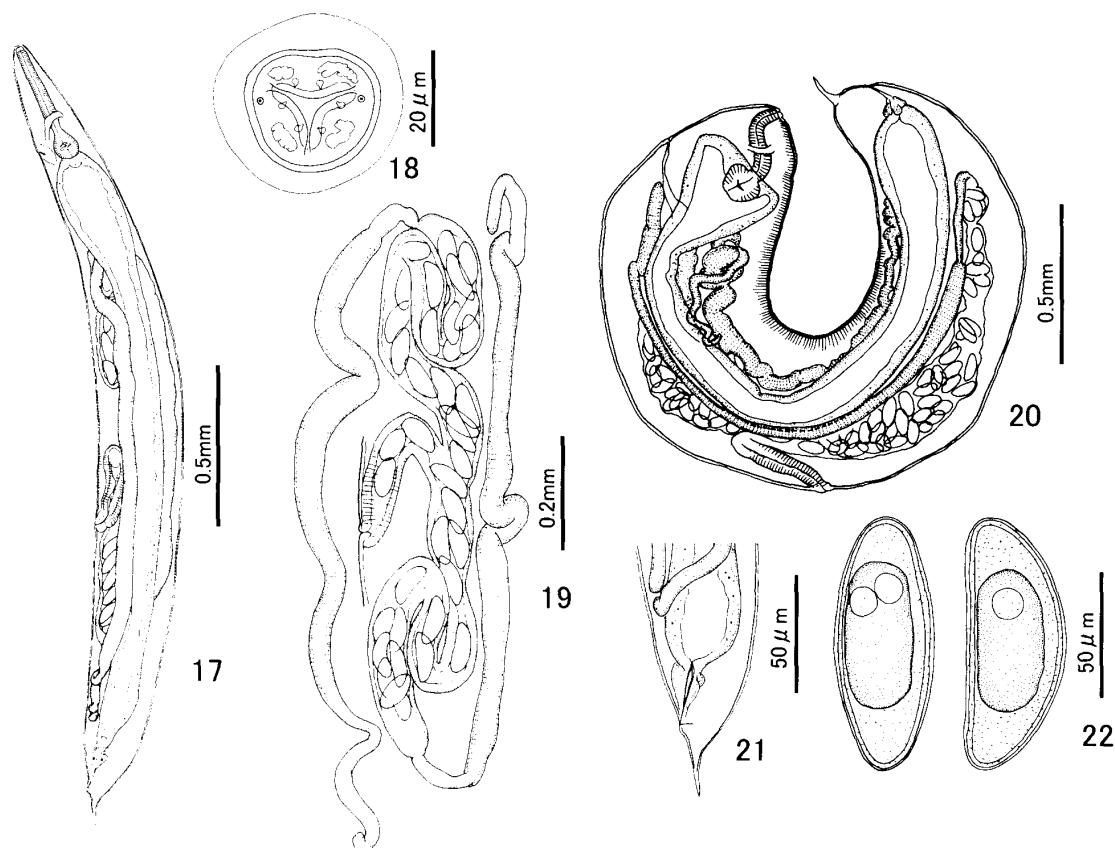
to midbody, 1.77 (1.29–2.34) mm, i.e., 60 (56–64) % of worm length, from cephalic end (Figs 17, 20). Vagina directed anteriorly; anterior branch of uterus connected to short anterior oviduct at level posterior to excretory pore; anterior ovary directed posteriorly and ending slightly anterior to anus; posterior branch of uterus connected to short posterior oviduct at level anterior to anus, terminating near level of anterior oviduct (Fig. 19). Tail conical, narrowed abruptly and forming pointed end, 145 (122–191) long (Figs 17, 20, 21). Eggs in uteri ellipsoidal, flattened on one side, light yellow in color, mean 98 ± 5 SD (90–110) by 36 ± 2 (32–40) ($n=50$), containing 1- or 2-cell-stage embryos at deposition (Fig. 22). Egg shell finely pitted on surface, with slightly thinner portion apically (Fig. 22).

Host. Japanese clawed salamander, *Onychodactylus japonicus*.

Site of infection. Small intestine.

Distribution. Hinoemata, Fukushima Prefecture, Honshu Island, Japan.

Remarks. Male polymorphism is often observed in pharyngodonids (cf. Chabaud and Golvan 1957; Ainsworth 1990). Usually the polymorphism is observed in the lateral alae and spicules whereas the arrangement of the genital papillae is rather stable. Male polymorphism of the present species was previously noticed by Hasegawa and Uchida (1986). The males described by Bursey and Goldberg (1999)



Figs 17–22. *Shunyanema japonicum* (Bursey and Goldberg, 1999), comb. nov., non-type female, from the Japanese clawed salamander, *Onychodactylus japonicus*. 17–19, 21, 22, MPM Coll. No. 18823; 20, MPM Coll. No. 18822. 17, Whole body of gravid worm, left lateral view; 18, cephalic end, apical view; 19, genital system, left lateral view; 20, full-grown worm, left lateral view; 21, posterior end, left lateral view; 22, eggs.

correspond to male morph I recognized in the present study in having wide lateral alae. The morph III male is a very peculiar form in its having many round formations of irregular size around the anus, but no genital papillae. This might represent an aberrancy rather than a morph.

The present worms are thinner than those of the type series described by Bursey and Goldberg (1999): width 115–153 in males with length of 0.62–1.17 mm; width 306–714 in females with length of 1.82–3.25 mm. However, our own observation of the paratypes revealed that those worms had been much flattened presumably due to coverslip pressure, resulting in a thicker than natural appearance.

The presence of oxyuroid nematodes in *Onychodactylus japonicus* was first noticed by Wilkie (1930), who suggested their affinity to the genus *Pharyngodon*. Pearse (1932) also recorded *Pharyngodon* sp. from *O. japonicus*. Neither of these authors gave a morphological description. We surmise that their worms are likely to have been *Shunyanema japonicum* because this species is rather common and no other oxyuroids have been identified from this salamander (cf. Hasegawa and Uchida 1986; Bursey and Goldberg 1999).

Discussion

Eight species of *Angiostoma* are parasitic in terrestrial gastropods (Morand and Barker 1995; Van Luc *et al.* 2005), while three species have been known from amphibians: *Angiostoma plethodontis* Chitwood, 1933 from salamanders, *Plethodon cinereus* (Green, 1818) and *P. richmondi* Netting and Mittleman, 1938, in North America; *Angiostoma chabaudi* (Cruz and Santiapillai, 1982) from caecilians, *Ichthyophis* spp., in Sri Lanka; and *Angiostoma onychodactyla* from *Onychodactylus japonicus* in Japan (Chitwood 1933; Cruz and Santiapillai 1982; Bursey and Goldberg 2000; Emery and Joy 2000; Kiontke and Sudhaus 2000). The presence of adult nematodes of a single genus in both mollusks and amphibians had been reported also for *Cosmocercoides* (cf. Adamson 1986). It was first mistakenly reported that *Cosmocercoides dukae* (Holl, 1928) is parasitic both in mollusks and anurans (cf. Anderson 1960), but later it was proven that the occurrence of *C. dukae* in anurans is accidental parasitism acquired by ingestion of infected mollusks (Bolek 1997; Anderson 2000).

Adamson (1986) suggested that the presence of *Angiostoma plethodontis* in the mentioned salamanders is also accidental parasitism resulted from ingestion of infected snails by the amphibian. However, *A. plethodontis* was found relatively commonly in *Plethodon richmondi* (prevalence 29.4%; Emery and Joy 2000). Association of *Angiostoma onychodactyla* with *Onychodactylus japonicus* is also often observed (prevalence 24%; Bursey and Goldberg 2000), although the salamander does not feed on snails (Pearse 1932). Moreover, Cruz and Santiapillai (1982) considered that parasitism of *Angiostoma chabaudi* in *Ichthyophis* spp. was not accidental. Hence it is surmised that *Angiostoma* has two lineages, which have adapted amphibians and mollusks respectively as hosts. DNA sequence analysis of *Angiostoma* spp. may be necessary to prove whether those in amphibians form a distinct clade from those in mollusks.

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References

- Adamson, M. L. 1981. *Parapharyngodon osteopili* n. sp. (Pharyngodonidae: Oxyuroidea) and a revision of *Parapharyngodon* and *Thelandros*. Systematic Parasitology 3: 105–117.
- Adamson, M. L. 1986. Modes of transmission and evolution of life histories in zooparasitic nematodes. Canadian Journal of Zoology 64: 1375–1384.
- Ainsworth, R. 1990. Male dimorphism in two new species of nematode (Pharyngodonidae: Oxyurida) from New Zealand lizards. Journal of Parasitology 76: 812–822.
- Anderson, R. C. 1960. On the development and transmission of *Cosmocercoides dukae* of terrestrial molluscs in Ontario. Canadian Journal of Zoology 38: 801–825.

- Anderson, R. C. 2000. *Nematode Parasites of Vertebrates. Their Development and Transmission*. Second edition. CABI Publishing, Wallingford, U.K., 650 pp.
- Anderson, R. C. and Lim, L. H. S. 1996. *Synodontisia moraveci* n. sp. (Oxyuroidea: Pharyngodonidae) from *Osteochilus melanopleurus* (Cyprinidae) of Malaysia, with a review of pinworms in fish and a key to species. *Systematic Parasitology* 34: 157–162.
- Bolek, M. G. 1997. Seasonal occurrence of *Cosmocercoides dukae* and prey analysis in the blue-spotted salamander, *Ambystoma laterale*, in southeastern Wisconsin. *Journal of the Helminthological Society of Washington* 64: 292–295.
- Burse, C. R. and Goldberg, S. R. 1999. *Parapharyngodon japonicus* sp. n. (Nematoda: Pharyngodonidae) from the Japanese clawed salamander, *Onychodactylus japonicus* (Caudata: Hynobiidae), from Japan. *Journal of the Helminthological Society of Washington* 66: 180–186.
- Burse, C. R. and Goldberg, S. R. 2000. *Angiostoma onychodactyla* sp. n. (Nematoda: Angiostomatidae) and other intestinal helminths of the Japanese clawed salamander, *Onychodactylus japonicus* (Caudata: Hynobiidae), from Japan. *Comparative Parasitology* 67: 60–65.
- Burse, C. R., McAllister, C. T. and Freed, P. S. 1997. *Spauligodon petersi* sp. n. and *Spauligodon smithi* sp. n. from lizards of Cape Province, South Africa. *Journal of the Helminthological Society of Washington* 64: 234–239.
- Chabaud, A. G. and Golvan, Y. J. 1957. Miscellaneous helminthologica Marocana XXIV. Nématodes parasites de lézards de la forêt de Nefifik. *Archives de l'Institut Pasteur de Maroc* 7: 447–469.
- Chitwood, B. G. 1933. On some nematodes of the superfamily Rhabditoidea and their status as parasites of reptiles and amphibians. *Journal of the Washington Academy of Sciences* 23: 508–520.
- Cruz, H. and Santiapillai, A. 1982. Parasites of the relict fauna of Ceylon. VIII. Helminths from *Ichthyophis* spp. (Amphibia: Gymnophiona). *Annales de Parasitologie Humaine et Comparée* 57: 317–327.
- Emery, M. B. and Joy, J. E. 2000. Endohelminths of the ravine salamander, *Plethodon richmondi*, from southwestern West Virginia, U.S.A. *Comparative Parasitology* 67: 133–135.
- Hasegawa, H. 2005. Two new genera of the Pharyngodonidae (Nematoda: Oxyuroidea) found in rhacophorid frogs of the Ryukyu Archipelago, Japan. *Journal of Parasitology* 91: 111–116.
- Hasegawa, H. and Uchida, A. 1986. Studies on the amphibian helminths in Japan. XIX. Nematodes from *Onychodactylus japonicus*. *Japanese Journal of Parasitology* 35 (supplement): 141. [In Japanese]
- Inglis, W. G. 1968. Nematodes parasitic in Western Australian frogs. *Bulletin of the British Museum (Natural History)* 16: 163–183.
- Kiontke, K. and Sudhaus, W. 2000. Phasmids in male Rhabditida and other secernentean nematodes. *Journal of Nematode Morphology and Systematics* 3: 1–37.
- Morand, S. 1986. *Angiostoma aspersae* n. sp. (Nematoda, Angiostomatidae), parasite de *Helix aspersa* Müller (Gastropoda, Helicidae). *Bulletin du Muséum National d'Histoire Naturelle, Paris*, (4) 8 (A, 1): 111–115.
- Morand, S. and Barker, G. M. 1995. *Angiostoma schizoglossae* n. sp. (Nematoda: Angiostomatidae) from the New Zealand endemic slug *Schizoglossa novoseelandica* (Gastropoda: Rhytididae). *Journal of Parasitology* 81: 94–98.
- Morand, S. and Spiridonov, S. 1989. Redescription de trois espèces d'Angiostomatidae (Nematoda, Rhabditida), parasite de Gastropodes Pulmonés Stylommatophores, et description

- du cycle évolutif de deux d'entre elles. Bulletin du Muséum National d'Histoire Naturelle, Paris, (4) 11 (A, 2): 367–385.
- Pearse, A. S. 1932. Parasites of Japanese salamanders. Ecology 13: 135–152.
- Petter, A. J. and Quentin, J. C. 1976. No. 4. Keys to genera of the Oxyuroidea. Pp. 1–29. In: Anderson, R. C. and Chabaud, A. G. (Eds) *CIH Keys to the Nematode Parasites of Vertebrates*. Commonwealth Agricultural Bureaux, Farnham Royal, Buckinghamshire, U.K.
- Petter, A. J., Vassiliades, G. and Troncy, P. M. 1972. Trois espèces d'oxyures parasites de poissons en Afrique. Annales de Parasitologie Humaine et Comparée 47: 569–579.
- Sengoku, S., Matsui, M., Hikida, T. and Nakaya, K. (Eds) 1996. *The Encyclopedia of Animals in Japan*. Vol. 5. *Amphibians, Reptiles, and Chondrichthyes*. Heibonsha, Tokyo, 189 pp. [In Japanese]
- Skrjabin, K. I., Shikhobalova, N. P. and Lagodovskaya, E. A. 1960. Oxyuroidea of animals and man. Part 1. In: Skrjabin K. I. (Ed.) *Essentials of Nematodology Vol. VIII*. Izdatel'stvo Akademii Nauk SSSR, Moskva, 588 pp. [In Russian; English translation 1974, Israel Program for Scientific Translations, Jerusalem, 526 pp.]
- Van Luc, P., Spiridonov, S. and Wilson, M. J. 2005. *Aulacnema monodelphis* n. g., n. sp. and *Angiostoma coloaensis* n. sp. (Nematoda: Rhabditida: Angiostomatidae) from terrestrial molluscs of Vietnam. Systematic Parasitology 60: 91–97.
- Wilkie, J. S. 1930. Some parasitic nematodes from Japanese Amphibia. Annals and Magazine of Natural History (10) 6: 606–614.